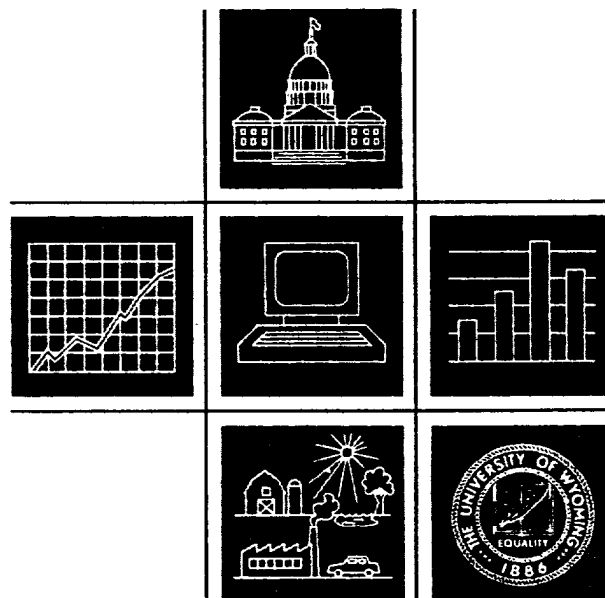


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Volume IV

VALUING ECOSYSTEM FUNCTIONS:
THE EFFECTS OF AIR POLLUTION

METHODS DEVELOPMENT IN MEASURING BENEFITS OF ENVIRONMENTAL IMPROVEMENTS

Volume IV

VALUING ECOSYSTEM FUNCTIONS: THE EFFECTS OF AIR POLLUTION

by

Thomas D. Crocker
John Tschirhart
Richard M. Adams
University of Wyoming
Laramie, Wyoming 82071

Richard W. Katz
National Center for Atmospheric Research
Boulder, Colorado 80307

USEPA Grant #CR808-893-01

Project Officer:

Dr. Alan Carlin
Office of Policy Analysis
Office of Policy, Planning and Evaluation
U.S. Environmental Protection Agency
Washington, D.C. 20460

OFFICE OF POLICY ANALYSIS
OFFICE OF POLICY, PLANNING AND EVALUATION
U.S. ENVIRONMENTAL PROTECTION AGENCY
WASHINGTON, D.C. 20460

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CHAPTER 1

INTEGRATING ECOSYSTEMS AND ECONOMICS

by

John Tschirhart and Thomas D. Crocker,
with assistance from S. Kask

SECTION 1

INTRODUCTION

Population growth and human territorial expansion are placing unprecedented burdens on ecosystems. While forests are being converted to farmlands, farmlands are being converted to suburbs. The Amazon forest, earth's richest biological region is losing to development each year an area half the size of Great Britain [Prance (1977)]. Pollution is now recognized as a global problem with particular emphasis on acid precipitation and the greenhouse effect. Estimates of species lost to extinction worldwide are as high as 1000 per year [Myers (1979)].

But what values are reflected by this and similar data on our dwindling natural environment? Part of the answer can come from a study of ecological systems placed in an economic framework. Ecological systems must be reduced to tractable analytical frameworks which can then be incorporated into economic models that are able to ascertain benefits and costs. For example, in environmental economics, studies have estimated the willingness to pay for trout fishing along a particular stream. These studies could then be used to estimate the value that the effect of a pollutant such as acid precipitation has on trout populations. Trout have value to people, and if the trout were to vanish so would the benefits of the fishing. But trout are only one species in a complex ecosystem. By removing other species, say certain insects that may appear to be of no value, the trout may also vanish. Thus, a proper valuation of an ecosystem entails not just the valuation of end products like trout, but a recognition of the interactions between trout and other species so that the value of these other species can be established. By doing this, better estimates can then be made of the uncompensated costs associated with population growth and industrial expansion which affect the sources of pleasure and life support services that ecosystem provide.

Ecosystems are incredibly complex. They may be composed of thousands of species interacting in diverse ways. Each species fills a niche in the overall system, and depends on one or more of the other species for survival. But complex systems are not foreign to economists who have the

difficult task of sorting out complex economies. Notions such as short-run and long-run equilibriums, steady states, and exogenous shocks appear to be applicable to both ecosystems and economies. For an economy, the economist uses models to determine the effect a tax in one sector has on other economic sectors. For an ecosystem, the ecologist (and the economist) may need to know the effect that a particular pollutant harming one insect species will have on all other species.

The parallels between ecosystems and economics suggest that similar models may be used for each. Moreover, if this can be accomplished, then linking ecosystems with economies is possible. Such a linkage would permit not only detailed descriptions of how a pollutant will effect an ecosystem, but how the changes brought about in the ecosystem will effect the economy and, in turn, how these changes in the economy will influence the ecosystem.

Ecologists attempt to answer such questions by using energy as a unit of value. By measuring the flow of energy through an ecosystem, one can determine how an exogenous shock might affect that energy flow [Grodzinski (1975)]. The effect is then evaluated using some pecuniary value placed on an energy unit. Some support for this approach once was found among economists. The English economist, J.A. Hobson (1929) has remarked that:

"...all serviceable organic activities consume tissue and expend energy, the biological costs of the services they render. Though this economy may not correspond in close quantitative fashion to a pleasure and pain economy or to any conscious valuation, it must be taken as the groundwork for that conscious valuation. For most economic purposes we are well-advised to prefer the organic test to any other test of welfare, bearing in mind that many organic costs do not register themselves easily or adequately in terms of conscious pain or disutility, while organic gains are not always interpretable in conscious enjoyment." (p. xxi)

According to one's perspective, Hobson's statement can be taken as support for an energetic basis of value, and as a plea for economists to devote more attention to the workings of the biological world and its implications for human welfare, both as a source of pleasure and as a life-support system. Hobson's first point has been received warmly by ecologists such as H.T. Odum (1971), to the point where it has been enshrined alongside cost-benefit analysis as a means of evaluating proposed energy technologies [Energy Research and Development Agency (1975)]. However, it has been coldly received by modern economists. Georgescu-Roegen (1979) neatly expresses the economists' source of difficulty with energy as the unit of value for the satisfaction of human wants:

"The entropic nature of the economic process notwithstanding, it would be a great mistake to think that it may be represented by a vast system of thermodynamic equations...The entropic process moves through an intricate web of anthropomorphic categories, of

utility and labor above all. Its true product is not a physical flow of dissipated matter and energy, but the enjoyment of life...pleasure is not related by a definite quantitative law to the low entropy consumed." (p. 1042)

The correct approach is therefore to include the ecosystem in the economy where the uses of the ecosystem can be evaluated relative to all other goods.

Hobson's second point, that economics should give deeper consideration to the role of biosphere in human affairs, has suffered from neglect. With the exception of the work inspired by Boulding (1966) and Krutilla (1967), the economics discipline continues to be notable for its inability to capture many of the concerns of biological scientists, particularly ecologists, about the impacts of human activities upon ecosystems and, via these ecosystem impacts, ultimately upon human welfare. Perhaps economists have dismissed these themes simply because the economics discipline has lacked a means of fitting them into the framework of economic analysis.

The purpose of this paper is to develop a link between ecosystems and economies that will allow an economic evaluation of ecosystem structure and diversity. We try to broaden traditional approaches to environmental economic problems by encompassing bioenergetics, but without resorting to the use of energy as the unit of value used by humans. There are two main phases of the development. First, an ecosystem model is described using the notions equivalent to production functions, optimization, and equilibria. Humans are absent from this phase. All energy input into the model derives from the sun. In the second phase, humans are introduced under the familiar guise of utility maximizers. This leads to behavior that interferes with the ecosystem through changes in the sources and uses of energy.

Section II develops a model of the optimizing behavior of a single organism in an ecosystem. Section III extends this idea to multiple organisms and to ecosystem equilibrium. Section IV suggests that there is empirical support for the results in Section III. Sections V, VI and VII introduce the economic problem. This is where human perspectives of the ecosystem enter. Section VIII introduces a methodology for valuing species. IX deals with ecological diversity.

SECTION 2

SINGLE ORGANISMS AS ENERGY MAXIMIZERS

Initially, a model of an ecosystem is developed where humans have neither a direct nor **indirect** influence. In this world, all energy is derived from the sun. Organisms may use this energy directly, in the case of plants, or indirectly, in the case of herbivores and carnivores. Each organism is a member of a particular trophic level, where a trophic level is defined as "...a collection of species which feed from the same set of sources and which do not produce for each other" [Hannon (1976, p. 260)]. In essence, each trophic level can be thought of as a stratum in a food pyramid. The objective is to link mathematically the trophic levels. This will provide a framework for discussing equilibria in the ecosystem.

Before deriving the links, however, the actions of the individual organisms must be described. In a general equilibrium model of an economy, individual consumers and firms are usually described as utility and profit maximizers, respectively. But in an ecosystem, do nonhuman organisms maximize? Can a weasel be credited with thoughtful preference revelation when it raids the chicken coop instead of ferreting out a mouse or two? "...men consciously optimize, animals do not - they survive by adopting successful strategies 'as if' conscious optimization takes place" [Hirschleifer (1977, p. 4)]. This "as if" assumption is sufficient to capture much of the behavior of nonhuman organisms, and, thereby, establish a fruitful model. Indeed, "as if" is the methodological basis adopted by many modern economists [Friedman (1953)].

Various suggestions have been made as to what it is that nonhuman organisms maximize, or behave as if they are maximizing. Lotka (1925) developed a model where the maximand is the rate of increase of the species. This rate is a function of food capture, shelter, and other physical needs. Obtaining these needs requires energy expenditure. Naturally, if a species is to be successful, then the energy expended on the needs must be less than or equal to the energy acquired. Lotka characterizes a maximum in this system with a set of equations where the marginal productivity (i.e., an increase in the species with respect to net energy input) of an energy expenditure equals the ~~marginal~~² loss (i.e., a decrease in the species) from that energy expenditure. Modern work has emphasized the role of energy more directly in the search for a maximand. Odum (1971, p. 90) points out that life requires power and "...the maximum and most economical collection, transmission, and utilization of power must be one of the principal selective criteria...". Finally, Hannon (1976) develops a model using stored energy as the maximand. Stored energy is simply the energy acquired by the organism less the energy needed to maintain itself. Hannon argues for the reasonableness of this objective

based on general observation, and on the increased organism stability it provides during periods of fluctuating inputs.

The stored energy approach is used here. It does not seem to differ significantly from Lotka's approach, particularly since he viewed organisms as energy transformers. If organisms of a species are successful in storing energy, this is interpreted as leading to an increase in the species' health and numbers. Hence, the stored energy approach appears acceptable to modern ecologists, and consistent with the pioneering work of Lotka.

For specificity, suppose the organism is a fox, which as an energy transformer, gathers all its energy from food, and then assimilates this energy for various purposes. All input energy must be accounted for as output energy in the form of waste heat, metabolism, growth, reproduction, losses to predators, detritus, mechanical activities, and storage. Let x_j and e'_j , $j = 0, \dots, n$, be the mass flow from the j th source to the organism and the energy content or caloric content per unit of mass j , respectively. Subscript $i = 0$ refers to the sun so that $e'_0 x_0$ is the energy that the fox absorbs directly from sunlight. Thus, x_0 can be thought of as time spent in sunlight and e'_0 the energy absorbed per unit of time. Many but not all species absorb energy directly from the sun. If a species does not then $x_0 = 0$. For simplicity, the sun is the only input that is not derived from another species. Therefore, subscripts $j = 1, \dots, n$ represents all species of plants and animals, and for the fox, a positive x_j , $j = 1, \dots, n$ implies that species j is prey. Total input energy is then:

$$\sum_{j=0}^n e'_j x_j \quad (1)$$

Let e''_j be the energy spent to obtain a unit of x_j , for example energy spent to run down a mouse, so that the net input of energy from a unit of x_j is $e_j = e'_j - e''_j$. Therefore, total net input energy is

$$\sum_{j=0}^n e_j x_j \quad (2)$$

For simplicity, all output energy will be captured by a single term. Accordingly,

$$e_{n+1} x_{n+1} \quad (3)$$

represents the above mentioned outputs with the exception of storage and predator losses. Again, e_{n+1} is a price per unit of mass loss x_{n+1} . Some outputs, such as heat loss, can be measured in energy units and e_{n+1} be one; however, no loss in generality results from using e_{n+1} . Predator losses are not considered here because they are beyond control of the fox; and if an individual fox is taken by a predator there is no maximization problem to discuss. In a sense, there is a zero/one solution to the fox's

problem. Predator losses are taken up in the next section.

Stored energy is the difference between input and output. It represents energy in excess of what is needed for maintenance. Letting r be stored energy, then from (2) and (3)

$$r = \sum_{j=0}^n e_j x_j - e_{n+1} x_{n+1} \quad (4)$$

Expression (4) is the objective function that the fox maximizes, and it is analogous to a firm's profit function. The chief difference is that a firm sells output to increase profits and purchases inputs which detracts from profits. The fox's outputs, such as heat loss, detract from stored energy while inputs contribute to stored energy.

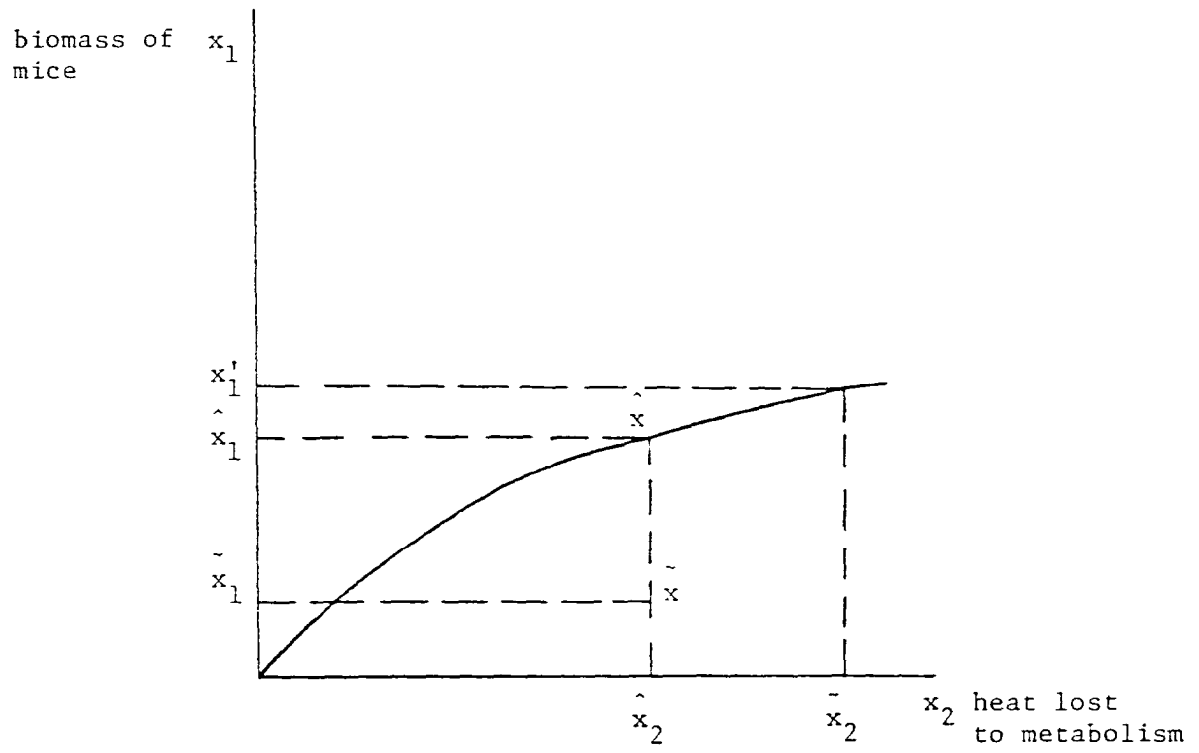
A bundle of inputs and outputs for the fox is represented by the real numbers $x = (x_0, x_1, \dots, x_n, x_{n+1})$. Not all bundles, however, are feasible for the fox. For instance, the fox cannot continually catch mice without ever losing heat energy. The set of feasible bundles will be called the physiology set. In essence, this set places constraints on what is achievable for the fox by describing the physiological processes which convert inputs to outputs. For example, as a general rule of ecology, in order for an organism to use ingested material, it must oxidize the organic molecules in the material it ingests [Morawitz (1968), Chap. 5]. This creates useful energy, but some formerly useful energy is also lost as heat. The physiology set depends on ambient temperature, time of year, and other environmental conditions, and human activities may be influential as well. Acid precipitation is a good example of a human activity that interacts with an ecosystem via alterations in physiology sets. For now, the set is assumed to be unchanging.

Several simple diagrams illustrate these notions. Suppose for the fox there is only one input, mice, and one output, metabolic heat loss. Figure 1 shows the physiology set as the shaded region. With metabolism of \hat{x}_2 , the fox can attain a quantity of mice \hat{x} , a quantity \hat{x} , or any amount between \hat{x} and the horizontal axis. Bundle \hat{x} represents the greatest amount of mice attainable for \hat{x}_2 . For this reason, \hat{x} is labelled an efficient point of the physiology set; and all points along the upper border of the set are referred to as the physiologically efficient points. Thus, a physiologically efficient bundle is one where greater mice biomass cannot be attained without even greater metabolism.

The dependency of the physiological set on environmental conditions is depicted in Figure 2. The cross-hatched area may represent the physiological set of a lake trout prior to the occurrence of acid precipitation, while the double cross-hatched region represents the trout's set subsequent to the acid precipitation. This change indicates a detrimental effect from the pollution, since the feasible set has been diminished.

For a fixed level of stored energy, \bar{r} , (4) can be plotted as the

Figure 1



straight line in Figure 3 labelled \bar{r} . A higher fixed level of stored energy is shown by the line r . The further these lines are above the origin, the greater is the stored energy. These lines can be referred to as iso-stored energy lines, since every point on any given line represents a combination of x_1 and x_2 that yield the same stored energy at the given energy prices. The vertical and horizontal intercepts are the stored energy in units of mice biomass and heat loss, respectively. The slope of the line is the ratio e_2/e_1 .

The fox is assumed to take e_1 and e_2 as given; that is, it has no control over these values and they enter as parameters in the maximization process. Maximum stored energy will be given by that iso-stored energy line that is furthest above the origin, but still having at least one point in common with the physiology set. Obviously, this point will be one that is physiologically efficient. Figure 4 illustrates maximums of \bar{r} for values \bar{e}_1 and \bar{e}_2 and, \hat{r} for values \hat{e}_1 and \hat{e}_2 . The maximizing solution depends on the shape of the physiology set and the values of e_1 and e_2 . The solution at $\hat{x} = (\hat{x}_1, \hat{x}_2)$ contains greater levels of heat loss and mice than $\bar{x} = (\bar{x}_1, \bar{x}_2)$, because biomass of mice has more energy content ($\hat{e}_1 > \bar{e}_1$) and/or metabolism results in less heat loss ($\hat{e}_1 < \bar{e}_1$). For values \bar{e}_1 and \bar{e}_2 , the fox would not move beyond point $\bar{x} = (\bar{x}_1, \bar{x}_2)$. To do so would mean more heat loss and more mice, but the energy gained would be less than the energy lost. For instance, moving from \bar{x} to \hat{x} at prices \bar{e}_1 and \bar{e}_2 would mean a drop in stored energy from r to \bar{r} . However, suppose mice were to become more plentiful, then e_1 would increase because e_1'' , the energy required to catch a mouse, would decrease. If (\bar{e}_1, \bar{e}_2) became (\hat{e}_1, \hat{e}_2) the fox would move to \hat{x} where stored energy increase from \bar{r} to \hat{r} .

A maximum will exist provided certain restrictions are placed on the physiology set. In particular, the set must be bound above and include its boundaries. These restrictions do not seem unrealistic in a real ecosystem. Figure 5 illustrates a set that is not bounded. For positive e_1 and e_2 , maximum stored energy is infinite since even higher iso-stored energy lines are feasible. The shape of the set must be left to experiments, observations, and statistical analysis, and it can be expected to vary significantly among organisms.

Further insights into the maximization model can be gained by returning to the general case. The concept of a physiology function is introduced using the physiology set. For any set of values of all but one of the net flows, x_j , there is only one value of x_j that is compatible with physiological efficiency. This is obvious for the two variable case from the above figures. For $n+2$ variables, let $x^{-j} = (x_0, \dots, x_{j-1}, x_{j+1}, \dots, x_{n+1})$, then there is a one-to-one correspondence between the $n+2-1$ dimension vector x^{-j} and the scalar x_j . In functional form,

$$x_j = f(x^{-j})$$

or equivalently

$$F(x) = x_j - f(x^{-j}) = 0 \quad (5)$$

Figure 2

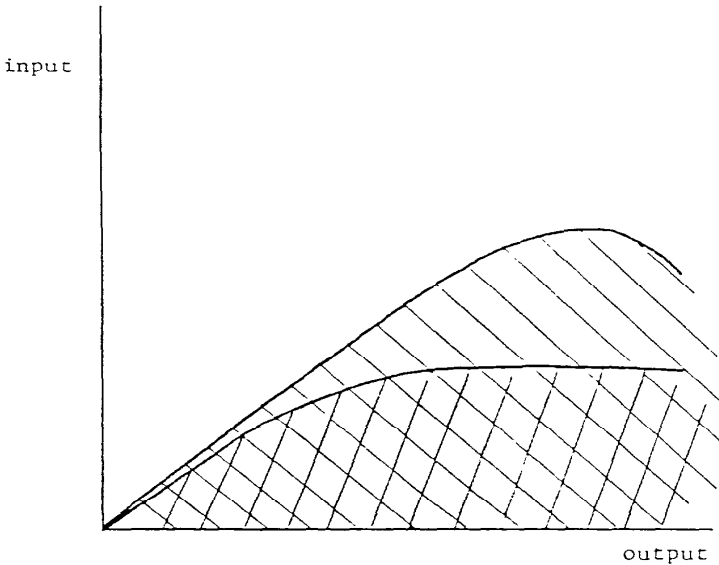


Figure 3

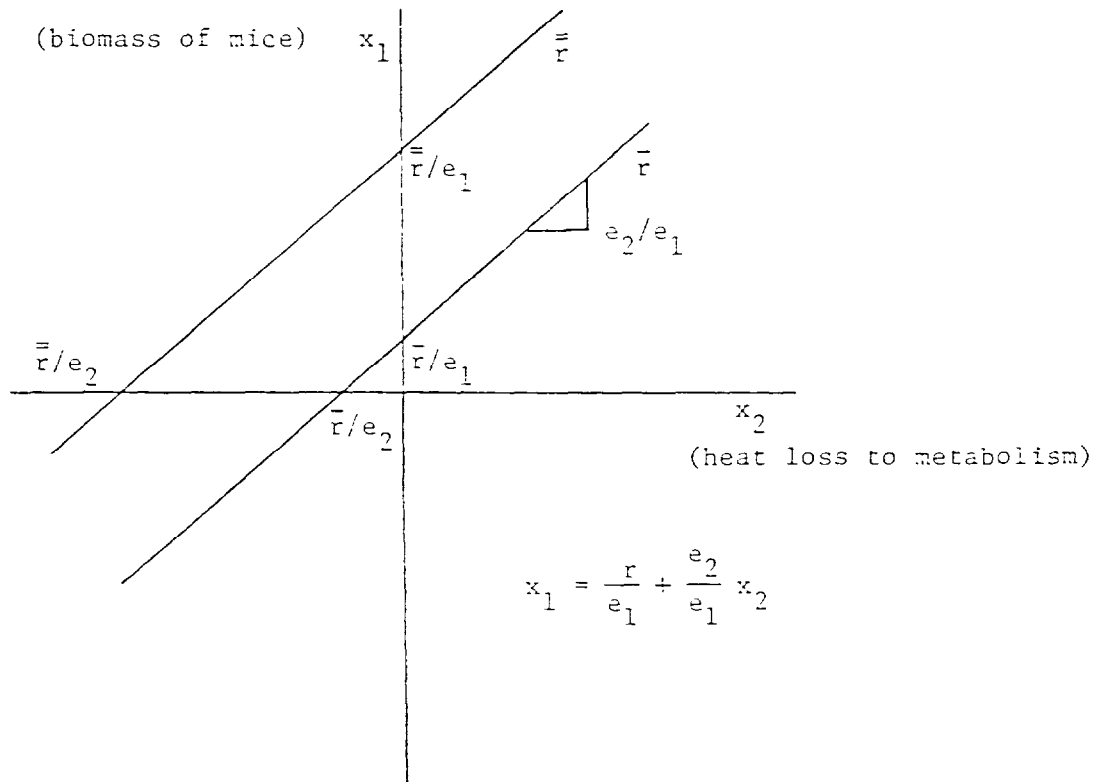
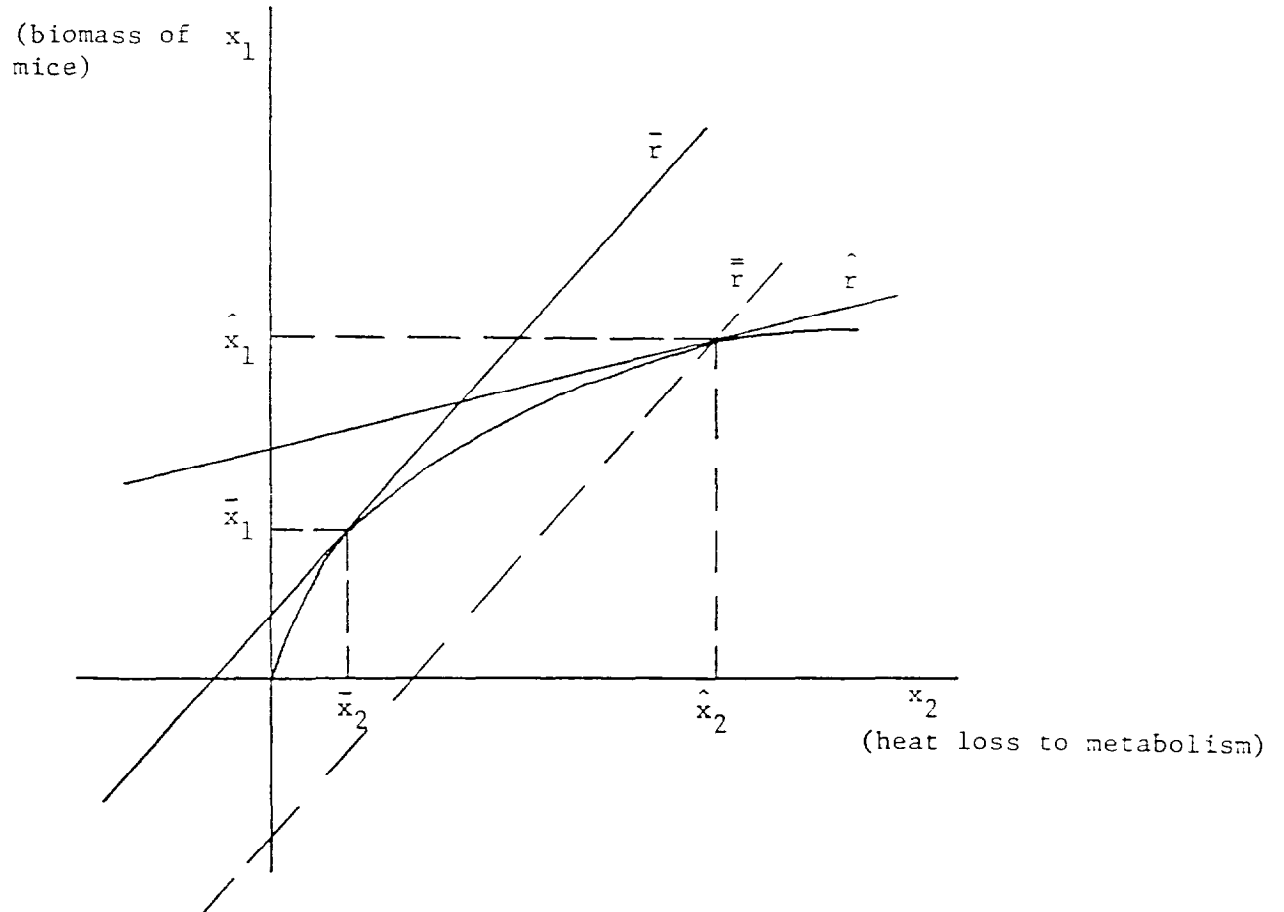


Figure 4



The function $F(x)$ is the physiology function, and, by construction, it embodies physiological efficiency. That is, \hat{x} is physiologically efficient if and only if $F(\hat{x}) = 0$. In two dimensions, $F(\hat{x}) = 0$ implies that \hat{x} is on the border of the physiology set.

The maximization problem can be restated as

$$\max r = \sum_{j=0}^n e_j x_j - e_{n+1} x_{n+1} \quad (6)$$

$$\text{subject to } F(x) = 0$$

where $F(x)$ is assumed to be twice differentiable and the physiology set is assumed to be strictly convex. Strict convexity assures that the second-order sufficiency conditions of the maximization problem are satisfied, and that there is a unique maximum. The Lagrangian for problem (6) is

$$L(x, \lambda) = r + \lambda F(x) \quad (7)$$

and the first-order conditions for a maximum are

$$x_j: e_j + \lambda \frac{\partial F(x)}{\partial x_j} = 0, \quad j = 0, \dots, \quad (8)$$

$$x_{n+1}: -e_{n+1} + \lambda \frac{\partial F(x)}{\partial x_{n+1}} = 0 \quad (9)$$

$$\lambda: F(x) = 0 \quad (10)$$

Dividing any two conditions in (8) by one another yields

$$\frac{\partial F(x)/\partial x_i}{\partial F(x)/\partial x_j} = \frac{e_i}{e_j} \quad (11)$$

so that for a maximum, the ratio of partial derivatives of $F(x)$ must be equal to the ratio of energy prices. Using (5),

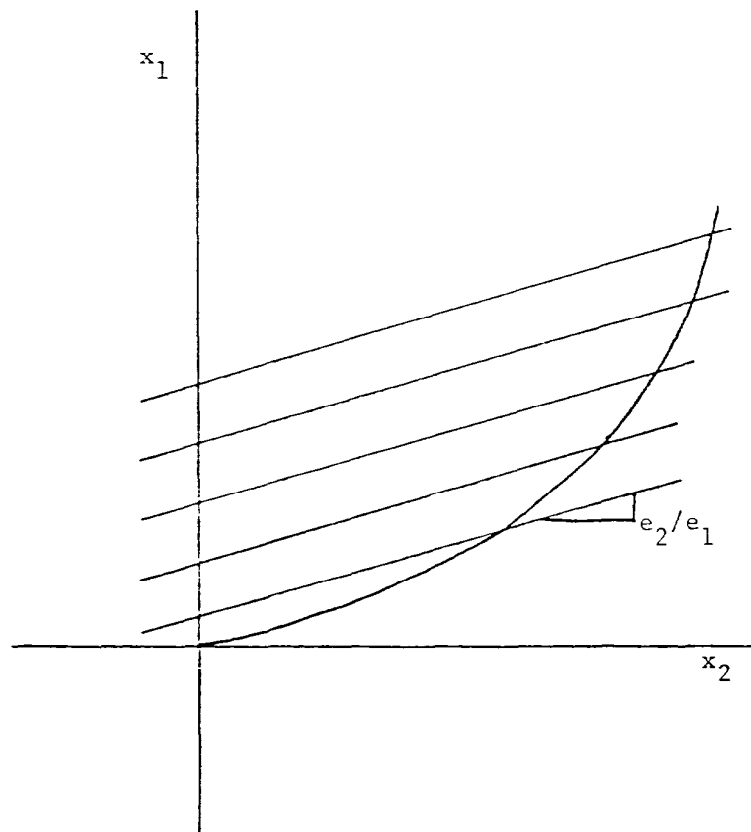
$$F(x_0, \dots, x_{j-1}, \bar{f}(x^{-j}), x_{j+1}, \dots, x_{n+1}) = 0$$

and differentiating with respect to x_i , $i \neq j$, yields

$$-\frac{\partial f(x^{-j})}{\partial x_i} = \frac{\partial F(x)/\partial x_i}{\partial F(x)/\partial x_j} \quad (12)$$

Thus, the left-hand-side of (11) can be interpreted as the rate at which x_j must be substituted for x_i while all other values are held constant. Or, ^j for the fox's predatory behavior, (11) states that the rate at which he can

Figure 5



trade mouse biomass for say rabbit biomass, while achieving the same stored energy must equal the ratio of the energy contents in units of mouse biomass and rabbit biomass. Alternatively, (11) and (12) can be used to obtain

$$-\frac{\partial e_j f(x^{-j})}{\partial e_i x_i} = 1 \quad (13)$$

The left-hand side of (13) is the rate at which energy from source j must be traded for energy from source i in order to be physiologically efficient. Or, substituting mice for rabbits must lower the input of rabbit energy at the same rate mouse energy is increased. To see the rationale behind this result, suppose the fox was obtaining more stored energy from the last unit of rabbit biomass than from the last unit of mouse biomass. Then (13) would be an inequality. The fox would begin to consume more rabbit biomass and less mouse biomass. Given the shape of the physiological function, eventually, the amount of mouse biomass given up for each unit of rabbit biomass consumed, and it must be given up with a fixed level of outputs (x_{n+1}), becomes so great that further rabbit biomass is undesirable. The tradeoff of mice for rabbits stops when (13) is satisfied as an equality.

In a similar fashion, (9) can be combined with any of the $n+1$ conditions in (8) to obtain

$$-\frac{\partial F(x)/\partial x_j}{\partial F(x)/\partial x_{n+1}} e_{n+1} = e_j \quad (14)$$

for $j = 0, \dots, n$. The interpretation is that all $n+1$ inputs are obtained such that their energy contribution to the metabolic processes are in proportion to their energy prices.

The first-order maximum conditions given by (8) - (10) constitute $n+3$ equations which can be solved for the optimum values of the x_0 and λ as functions of the energy prices. A solution is guaranteed by the assumption of a convex physiology set. Thus, there exist the functions:

$$x_j = x_j(e) \quad j = 0, \dots, n+1 \quad (15a)$$

$$\lambda = \lambda(e) \quad (15b)$$

The function $x_j(e)$ indicates the amount of the j th input acquired or j th output spent, given the energy prices of all inputs and outputs. Substituting these amounts back into the objective function gives the maximum stored energy,

$$r = \sum_{j=0}^n e_j x_j(e) - e_{n+1} x_{n+1}(e) \quad (16)$$

If j represents rabbits, $x_j(e)$ can be thought of as the fox's demand for rabbits at prices 2.

Finally, the $x_j(e)$ terms can be substituted into (8) - (10) and derivatives can be taken with respect to the e_j . This yields the system of equations:

$$\begin{bmatrix} 0 & F_0 & F_1 & \dots & F_{n+1} \\ F_0 & 1+\lambda F_{00} & \lambda F_{01} & & \lambda F_{0n+1} \\ F_1 & \lambda F_{01} & 1+\lambda F_{11} & & \\ \vdots & \vdots & & & \\ F_{n+1} & \lambda F_{0n+1} & & -1+\lambda F_{n+1 \ n+1} & \end{bmatrix} \begin{bmatrix} \lambda_0 & \lambda_1 & \dots & \lambda_{n+1} \\ x_{00} & x_{01} & \dots & x_{0n+1} \\ x_{10} & x_{11} & & \\ \vdots & & & \\ x_{n+10} & & & x_{n+1 \ n+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & \dots & 0 \\ -1 & 0 & & 0 \\ 0 & -1 & & \\ 0 & 0 & & \\ \vdots & \vdots & & -1 & 0 \\ 0 & 0 & \dots & 0 & 1 \end{bmatrix}$$

(17)

where subscripts indicate partial derivatives. For instance, $x_{ij} = \partial x_i(e) / \partial e_j$. This system can be used in a comparative static analysis (see e.g., Chiang) to solve for the $\partial x_k(e) / \partial e_j$ values to obtain

$$\frac{\partial x_j(e)}{\partial e_j} > 0 \quad j = 0, \dots, n \quad (18)$$

$$\frac{\partial x_{n+1}(e)}{\partial e_{n+1}} < 0 \quad (19)$$

The interpretations of (18) is that an increase in the energy price of a net input results in an increase in the use of that input, ceteris paribus. If the net energy the fox could obtain from rabbit biomass were to increase while the net energy obtained from mouse biomass remained the same, the fox would chase more rabbits and fewer mice. A similar interpretation holds on the output side and (19).

SECTION 3

MULTIPLE ORGANISMS AND NATURAL EQUILIBRIUM

The individual organism in the previous section must now be placed in the context of an entire ecosystem. Each organism belongs to a species, and sets of species form trophic levels. The trophic levels are links in a food chain or levels in a hierarchy. Species may feed on other species in lower trophic levels, and in turn may provide substance for species in higher trophic levels.

To simplify the following analysis and to avoid notational complexity of defining the ecosystem, individual organisms will be aggregated to the species level. Thus, the collective goal of an entire species is to maximize stored energy which is the sum of stored energy for all the organisms in the species. This also avoids certain complications that occur when, say a bobcat consumes a rabbit. The bobcat receives an input but the rabbit is gone. At the species level, however, the bobcats collectively receive an input, while the rabbits collectively yield an output.

In aggregating, all individuals in a species are assumed identical; that is, their physiological functions are the same. This avoids having to consider the distribution of resources among individuals, and a single physiological function can be used for an entire species. The problem for species i is to

$$\begin{aligned} \text{maximize } R_i &= \sum_{j=0}^n E_{ji} X_{ji} - \sum_{j=1}^n E_{ij} \bar{X}_{ij} - E_{i,n+1} X_{i,n+1} \quad (20) \\ \text{s.t. } F^i(X_i, \bar{X}_i) &= 0 \end{aligned}$$

where R_i is the species stored energy E 's are the energy prices, x_{ji} 's are inputs in the first summation and \bar{x}_{ij} 's are outputs to other species in the second summation, n is the number of species, x_i is a vector whose elements are the x_{ji} and $x_{i,n+1}$, and the bar notation on x_{ij} is to indicate that outputs to other species are fixed. Most of these terms require a more detailed discussion. In general for outputs and inputs, X_{ij} , $i, j=1, \dots, n$, is the output of the i th species to the j th species. Thus it is an input to the j th species. The \bar{X}_{ij} 's enter parametrically into a species physiological function. If these outputs were decision variables, the species would set their values to zero; therefore, these outputs are fixed. They are exogenous to the individual species, but endogenous in the entire ecosystem since they are inputs of other species. For example, oak trees cannot avoid having squirrels consume their acorns; therefore, the output

of acorns to squirrels is fixed in the oak trees' maximization problem.

Figure 6 illustrates the effect of these fixed outputs on the fox species' physiological function. The axes are the same as in the previous section, except that they represent aggregates for the entire fox species. Also, \bar{X}_3 is an output to a predator of foxes. When \bar{X}_3' of fox biomass is sacrificed to predators, an input of X_1 mice requires metabolism of X_2' . But when $\bar{X}_3'' > \bar{X}_3'$ is lost to predators, the function shifts downward and a greater metabolic level, X_2'' , is required for the same input of mice. Basically, the greater metabolic level is needed to support the additional fox biomass taken by predators.

Where there is no direct interaction between species i and j then $\bar{X}_{ji} = x_{ji} = 0$. If $X_{ji} > 0$ then $\bar{X}_{ji} = 0$; that is, if species i feeds on species j , then j does not feed on i . This is not universally true, however, it leads to less notation in the model. As in the previous section, the zero index in the first summation of (20) indicates incoming solar energy, and the $n+1$ index indicates output, such as heat loss to the physical environment and not an input to another species.

The E 's are energy prices as discussed in the previous section. In the case where predator in species i captures prey in species j , X_{ji} units of biomass are transferred to the predator. This biomass contains $E_{ji} X_{ji}$ energy units. Since the predator must also expend energy in the capture, $E_{ji} X_{ji}$ is the net energy gained by the predator or as in the last section

$$E_{ji} X_{ji} = (E'_{ji} - E''_{ji}) X_{ji} \quad (21)$$

All energy prices are parametric in that every species takes the prices as given.

A natural equilibrium of the ecosystem, where natural refers to no human intervention, is provided by the simultaneous solution of all species' first order conditions. Each species provides at most $n+2$ equations from its $n+1$ input variables ($X_{0i}, X_{1i}, \dots, X_{ni}$) and one input variable ($X_{i,n+1}$). There may be fewer if there is no direct interaction with some species. In total, there are at most $n \times (n+2)$ equations and variables. In the long-run, all species will have zero stored energy. The driving force for this outcome is the change in prices that occur when stored energies are nonzero. For example, suppose $R_i > 0$. Then E_{ij} for $j = 1, \dots, n$ will decrease, since species i is bountiful and more easily preyed upon. As more predation occurs, R_i will tend towards zero. A similar but reverse story can be told for $R_i < 0$.

This ecosystem can be likened to an economic system. A storage maximizing species is like a profit maximizing firm, and the firm sells outputs to other firms and buys inputs from other firms. The physiological function is like the firm's production function. One distinction is the presence of the \bar{X} terms which have no counterparts in economic models. But this is because economic models deal with voluntary trades, involuntary

trades are largely ignored. Involuntary trades are an essential part of the ecosystem. Mice do not volunteer themselves as inputs to the fox.

Provided certain conditions are met on species' physiology functions (i.e., strict quasi-concavity), the first-order conditions for stored energy maximization (conditions comparable to (8), (9), and (10)) can be inverted to obtain continuous, differentiable input demand functions. Species i 's demand for biomass from organism j is

$$x_{ji}(E, \bar{X}) \quad (22)$$

Where E represents all the energy prices as defined above and \bar{X} are the exogenous outputs supplied by i to other species. Using comparative static analysis, it can be shown that

$$\frac{\partial x_{ji}}{\partial E_{ji}} > 0 \quad (23)$$

for $j = 1, \dots, n$. Thus, an increase in the energy content per unit of j 's biomass (E'_{ji}) or a decrease in the energy spent to obtain a unit of j 's biomass (E''_{ji}) will result in an increase in demand for species j by species i . Other comparative statics results will have signs dependent upon the complementarity between inputs and outputs in the physiological function. These signs are not unequivocal without placing further restrictions on the function.

Finally, as was done for (16) and the individual organism, the demands can be substituted into the original objective function for each species to obtain a stored energy function. Thus, for species i , $i = 1, \dots, n$:

$$R_i(E, \bar{X}) = \sum_{j=0}^n E_{ji} x_{ji}(E, \bar{X}) - \sum_{j=1}^n E_{ij} \bar{X}_{ij} - E_{i,n+1} X_{i,n+1}(E, \bar{X}) \quad (24)$$

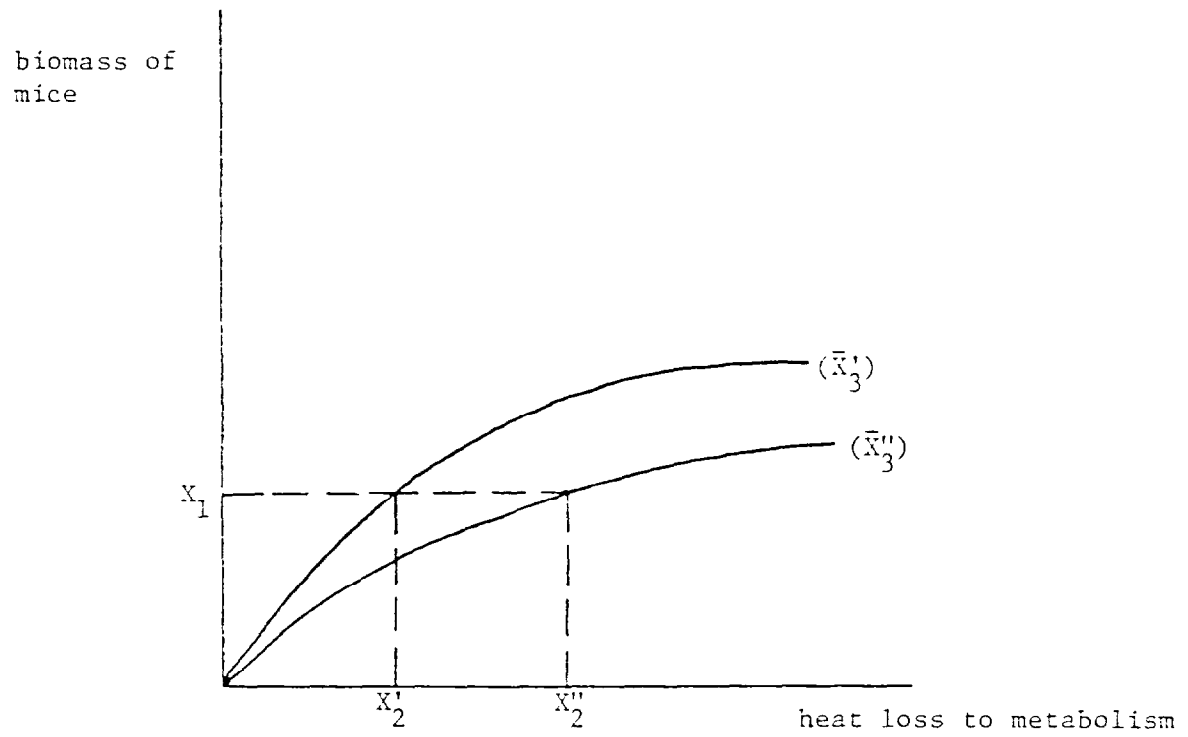
The function R_i gives the maximum stored energy possible for species i over all values of input/output prices and outputs. The envelope theorem can be used to show

$$\frac{\partial R_i}{\partial E'_{ji}} = - \frac{\partial R_i}{\partial E''_{ji}} = x_{ji} > 0, \quad \frac{\partial R_i}{\partial E_{ij}} = -\bar{X}_{ij} < 0 \quad (25)$$

Thus, if species i and j interact, increased energy content per unit of biomass of input species j , or decreased energy expenditures for obtaining units of biomass from species j , or decreased energy content of biomass yielded to species j will result in increased stored energy. Additionally,

$$\frac{\partial R_i}{\partial X_{ij}} = -E_{ij} + \frac{\lambda \partial F^i}{\partial X_{ij}} < 0 \quad (26)$$

Figure 6



so that increases in exogenous outputs to predators have negative effects on stored energy. This follows from Figure 6 where increased predation always decreases the feasible region for the species.⁵ As noted below, this is a short-run effect; that is, increased predation immediately lowers stored energy of the species. In the long run, as the ecosystem seeks a new equilibrium, certain prices may adjust and stored energy may increase. Witness the human practice of culling species to increase stability and productivity.

SECTION 4

EMPIRICAL SUPPORT FOR THE ECOSYSTEM MODEL

A central result in the previous Section is the derivation of the input demand function of one species for another. That is, $X_{ij}(E, \bar{X})$ is the i th species demand for the biomass of organism j . Moreover (23) showed that the partial of X_{ij} with respect to E_j is positive (inequality (23)). This result constitutes a testable hypothesis which, if verified, lends support for the theory developed above. In economics, one would test equivalent hypothesis about consumer demand by gathering primarily price, quantity, and income data, and using econometric techniques to estimate a demand function. Testing the ecosystem hypothesis given by (23) requires gathering the appropriate data and, if the data is adequate, using econometric techniques to estimate the demand function of one species for another. In this Section, the data requirements are discussed, and shortfalls in data cited. However, a number of biological studies are cited which do lend support for the ecosystem model.

Result (23) implies that an increase in the energy content per unit of species j 's biomass (E_j) or a decrease in the energy spent to obtain a unit of j 's biomass (E_{ij}) will result in an increase in demand for species j by species i . Thus data requirements include; i) the energy content per unit of all prey species' biomass; ii) the energy spent to obtain a unit of all prey species' biomass. The former requires studies to determine how the energy content varies over measures of biomass for the prey species. A reasonable proxy here might simply be to use a measure of weight such as pounds of the prey. The latter data is more vexing. However, a reasonable proxy here would be some measure of the availability of the prey. An abundant prey species would require less energy to be spent in capture than a nonabundant prey species, assuming both species have similar escape responses. One possibility is to use the reciprocal of the abundance of biomass per unit area as a measure of the energy price.

In addition to the price, (22) shows that the exogenous outputs are also variables in the demand function. This would require obtaining a measure of the biomass loss of the predator species to its own predators.

These various data are not always readily available or in a useful form. Some studies provide information on the quantities of various foods consumed by certain species, but do not indicate the relative abundance of these foods. An example would be a study by Baker and Hobbs (1982) which tabulated various plant species consumed by elk in Colorado. A study that does collect the correct type of data is one by Wallmo et al. (1977). They examine deer diet and habitat in Colorado. They list the different forage consumed; they tabulate the relative abundance of the forage consumed; and

they then document how the forage breaks down into crude protein, carbohydrates, cellulose, etc. While this qualitatively satisfies the data requirements, the quantity of data is too scanty for an econometric analysis. Kufeld (1973) documents forty eight papers that study food habits of elk, and ranks the various foods in the elk's diet according to their value of the elk. This borders on the type of data requirements useful to economists, and may be adequate for econometric analysis.

A number of papers have used laboratory experiments to test hypothesis of the type given by (23). On one hand, laboratory experiments have an advantage in that other variables (weather, age of organisms, etc.) can be held constant. On the other hand, this is no guarantee that behavior is not modified in a laboratory setting.

Rapport (1971) uses microeconomic techniques to examine the foraging behavior of certain protozoan. His purpose is to show that the "fundamental theorem" of foraging theory, that predators rank order single prey species, can be improved upon using economic techniques. In particular, he argues that predators choose among alternative bundles of prey. Moreover, while the "fundamental theorem" implies that changes in relative abundance of less desired prey has no effect on foraging, Rapport shows that changes in relative abundance of any prey species effects foraging. His experiments consisted of allowing protozoan to feed for one hour in the presence of varying densities of two algae prey species. A clear pattern emerged whereby greater densities of a species led to greater consumption of that species as (23) would dictate.

In another laboratory experiment, Kagel et al. (1975) observed the behavior of white rats. Specifically, the rats were allowed to push one of two levers, where one lever delivered rootbeer and the other Collins mix. Each rat was allowed so many pushes on the levers and initially 20 pushes were required on either lever to obtain a unit of liquid. At these prices, different rats chose different combinations of rootbeer and Collins mix. Then the prices were changes and 40 pushes were required for rootbeer and 10 for Collins mix. Each rat was provided with enough total pushes so that the original consumption bundle was possible. The result was as (23) would predict. All rats increased consumption of Collins mix and decreased consumption of rootbeer. Thus, goods are not ranked one at a time, but rather bundles of goods are ranked and the highest ranked bundle in the opportunity set is consumed.

Finally, there have been nonlaboratory studies that also lend support to the hypothesis presented above. Menge (1972) observed the foraging strategy of starfish. The observations were conducted over a period of about two years in the San Juan Islands off Washington. Menge analyzed the starfish diet by both numerical and caloric consumption and he observed that they consumed more of a type of cirripede in the summer and autumn when the cirripede was more abundant. The increased abundance results in a reduction in the expended energy of the starfish and an increase in demand. Menge also found that the starfish consumed large amounts of a certain gastropod which can be explained by the ease with which the gastropod is captured. Generally, he found that prey species with less effective escape

responses were consumed more often than those with more effective escape responses.

In another study, Werner and Hall (1974) examined bluegill sunfish predation on three different size groups of daphinea. The authors observed that as the density of prey increased for all groups, the sunfish began to select only the largest prey. Goss-Custard (1977) had similar findings with the foraging habits of redshark.

Bar-tailed godwits were studied by Evans (1976) who observed that the birds used less costly foraging methods when prey was scarce, thereby reducing expended energy. In fact, he found that foraging may completely stop when prey is very scarce, presumably because net energy from preying may actually be negative.

SECTION 5

HUMAN INTERVENTION

The natural ecosystem is characterized by inputs, outputs, energy prices, and physiology functions. Humans intervene in the ecosystem by directly or indirectly effecting all of these characteristics. Humans also change in the overall energy equation, since total energy into the ecosystem does not originate only with the sun. Instead, stored energy or fossil fuels are another source.

Examples of human intervention are given in Table 1. In fact, virtually any human action will have some influence on the ecosystem either directly or indirectly through one or more of the listed characteristics. The objective here is to capture this influence by augmenting the natural ecosystem model.

Initially, the analysis will be confined to the effects of human inputs and outputs. Humans have initial endowments of s raw materials to be used in the production of ecosystem goods and m manufactured goods. In turn, these ecosystem goods are also used in the production of manufactured

Table 1

	<u>Physiology Functions</u>	<u>Energy Prices</u>	<u>Inputs/Outputs</u>
Agriculture, Ranching	Developing new breeds of domestic plants and animals	Tilling the soil to make nutrients more accessible	Adding fertilizer
Timber	Breeding faster growing trees	Creating mono- cultures that decrease diversity and alter prices of food search	Cropping the forests
Hunting, Fishing	Fish hatcheries developing new breeds of wild fish	Creates higher prices for pred- ators of the hunted species	Cropping and stocking
Pesticides	Interfering with birds' of prey ability to produce	Raising energy prices of food search by insect predators	Eliminating insect species

goods. Let $Z = (Z_1, \dots, Z_m)$ be manufactured goods, and let Y_{pq}^z be the amount of raw input p used in the production of Z_q . Furthermore, let Y_{pi}^h be the amount of raw input p used as an input to the i th species. Then, if \bar{Y}_p is the initial endowment of raw input p , it follows that

$$\sum_{q=1}^m Y_{pq}^z + \sum_{i=1}^n Y_{pi}^h = \bar{Y}_p \quad (27)$$

for $p = 1, \dots, s$.

The problem for the i th species given by (20) can now be rewritten as

$$\text{Maximize } R_i^h = R_i + \sum_{p=1}^s E_{pi}^h \bar{Y}_{pi}^h \quad (28)$$

$$\text{s.t. } F^i(X_i, \bar{X}_i, \bar{Y}_i) = 0 \quad (29)$$

The stored energy in the **interventionist** state is rewritten as R_i^h to denote human presence. The inputs, Y_{pi}^h , that have been appended to the objective function are fixed for every species. This is to say that species have no control over how humans supply inputs, as the oak tree has no control over squirrels pilfering acorns.

Humans export biomass from the ecosystem to be used as inputs in the production of manufactured goods. Agriculture is a good example. A manufactured good may be a tomato in the supermarket. The ecosystem provides a tomato on the vine which is then combined with other resources (labor, transportation, etc.) to produce the manufactured good. This exportation or cropping is done from stored energy. "...cropping from storage (is) removing from the system a constant fraction of that energy which is being diverted into storage" [Hannon (1976), p. 260]. The species continues to maximize stored energy which is modified as

$$R_i^h = (1 - c_i) [R_i + \sum_{p=1}^s E_{pi}^h \bar{Y}_{pi}^h] \quad (28')$$

In (28'), c_i is the fraction of stored energy being cropped. Also, $0 \leq c_i \leq 1$ where $c_i = 1$ implies all stored energy is diverted to humans as in some agricultural products (wheat, vegetables, and other annuals) and $c_i = 0$ implies no human cropping. The actual amount of cropped stored energy from the i th species is denoted by

$$c_i [R_i + \sum_{p=1}^s E_{pi}^h \bar{Y}_{pi}^h] = c_i A_i \quad (30)$$

The c_i are fixed at levels that maintain the viability of the species. In other words, too much cropping may lead to instability in the species, but this possibility will be ignored at this point.

Species' demand for biomass are now dependent on the human inputs as well. Thus, (22) becomes

$$X_{ji}(E, E^h, \bar{X}, \bar{Y}^h) \quad (31)$$

where the human associated energy price vector E^h and input vector \bar{Y}^h are additional arguments. The maximum stored energy function of species i becomes

$$R_i^h(E, E^h, \bar{X}, \bar{Y}^h) = (1 - c_i)A_i(E, E^h, \bar{X}, \bar{Y}^h) \quad (32)$$

And by the envelope theorem,

$$\frac{\partial R_i^h}{\partial \bar{Y}_{pi}^h} = (1 - c_i) \left[E_{pi}^h + \lambda \frac{\partial F_i^h}{\partial Y_{pi}^h} \right] \gtrless 0 \quad (33)$$

so that changes in human inputs to a species have ambiguous effects on stored energy. The ambiguity arises because humans may be supplying too much or too little input given the species' objective of storage maximization.

SECTION 6

THE ECONOMIC PROBLEM

The economics problem is to allocate the raw inputs among manufactured goods and the ecosystem to maximize human welfare. A community welfare function will be used to represent human preferences. The function is written as

$$U(Z_1, \dots, Z_m, R_1^h, \dots, R_n^h) \quad (34)$$

Humans derive utility from manufactured goods and directly from the species in the ecosystem. The latter sources of utility refer to enjoying (or not enjoying) nonconsumptive qualities of the ecosystem. Included are aesthetics, studying plants and animals, camping, photography, and so on (not enjoying refers to insect attacks, aversion to snakes, etc.). These activities are enhanced by a healthy ecosystem, and stored energy is assumed to be a reasonable proxy for health. Let $U_q = \partial U / \partial Z_q$ for $q = 1, \dots, m$ and $U_{hi} = \partial U / \partial R_i^h$ for $i = 1, \dots, n$. Nonsatiation for manufactured goods implies $U_q > 0$ for $q = 1, \dots, m$. For the ecosystem, however $U_{hi} > 0$ for species providing nonconsumptive enjoyment (maple trees, deer, etc.), $U_{hi} = 0$ for species that are virtually unnoticed (soil microbes, lichens: etc.), and $U_{hi} < 0$ for pest species (weeds, mosquitoes, etc.).

For species that are used as inputs to manufacturing, humans essentially view the output from those species ($c_i A_i$) as a production function that depends on the raw inputs supplied to these species. That is, raw inputs are supplied, the species solves its stored energy maximization problem, and then yields output to the humans. While the humans are not cognizant of the intricacies involved in stored energy maximization, they are aware of the approximate amount of species output available for a given raw input. A farmer knows reasonably well the yield of corn from a given amount of fertilizer, although knowledge of the corn's physiology and other inputs and outputs is unnecessary. That humans do not know precisely the species' output from a given input can be attributed to uncertainties (e.g., weather in agriculture) and lack of knowledge about ecosystem interactions. Uncertainties are beyond the scope of this work, but the lack of knowledge will be discussed below as ecosystem externalities. One further simplification is made to avoid notational complexity. The ecosystem is comprised of n species that form a very simple food chain. Species i , $i = 1, \dots, n$, receives inputs, or demands outputs, from species $i - 1$ only. Where $i = 1$, the species only obtains input from the sun. Although this masks much of the richness of the ecosystem interactions, it suffices to show how human intervention can reverberate through the ecosystem. Given this assumption, the stored energy for species i can be written

$$R_i^h = E_{i-1,i} X_{i-1,i} - E_{i,i+1} \bar{X}_{i,i+1} - E_{i,n+1} X_{i,n+1} \quad (35)$$

Manufactured goods are produced using raw inputs and ecosystem inputs. Production of the qth good is given by the function

$$Z_q = G^q(Y_{1q}^z, \dots, Y_{pq}^z, c_{iq} A_{iq}, \dots, c_{nq} A_{nq}) \quad (36)$$

where $c_{iq} A_{iq}$ is the cropped stored energy from species i used in the production of the qth good.

The human problem can now be stated as maximizing welfare given by (34) subject to the functional relations given by (32) and (36) and endowment conditions from (27). Maximization is over all raw inputs. The maximum is characterized by the following expression which shows the case where $Y_{pi}^h > 0$ and $Y_{pq}^a > 0$, that is, positive amounts of raw input p are used as input for species i and for manufactured good q:

$$U_q \frac{\partial G^q}{\partial Y_{pq}^z} = U_{hi} \frac{\partial R_i^h}{\partial Y_{pi}^h} + \left\{ \sum_{j=1}^i U_{hj} \frac{\partial R_j^h}{\partial X_{j-1,j}} \prod_{k=j}^{i-1} \frac{\partial X_{k-1,k}}{\partial X_{k,k+1}} \right\} \frac{\partial X_{i-1,i}}{\partial Y_{pi}^h} +$$

$$\left\{ \sum_{q=1}^m U_q \sum_{j=1}^i \frac{\partial G^q}{\partial c_{jq} A_{jq}} \frac{\partial c_{jq} A_{jq}}{\partial X_{j-1,j}} \prod_{k=j}^{i-1} \frac{\partial X_{k-1,k}}{\partial X_{k,k+1}} \right\} \frac{\partial X_{i-1,i}}{\partial Y_{pi}^h} \quad (37)$$

Basically, (37) states that raw input p should be distributed in such a way that the marginal benefits of its use in manufacturing (left hand side (l.h.s.)) should equal the marginal benefits of its use as an ecosystem input (right hand side (r.h.s.)). Specifically, the first term on the l.h.s. is the marginal utility from the change in the qth manufactured good as the pth raw input to this good is changed. The first term on the r.h.s. is the marginal utility of a change in the ith species' stored energy due to changing the pth raw input to this species. The second term on the r.h.s. is the marginal utility of a change in stored energy of all lower species due to changing the pth raw input to the ith species. For example, if the food chain consists of three species, mayflies (1), trout (2), and eagles (3), then a human input to the eagles will effect eagle stored energy and the associated utility - the first term on the r.h.s. In turn, the eagles' demand for trout, the trout's demand for mayflies, and the mayflies' use of solar energy are all effected. Thus, the stored energy in all three species is effected which is then reflected in utility changes. All of these effects are captured in the second term. The third term is the sum of marginal utilities for all manufactured goods as the production of these goods is altered by the stored energy changes in all the species lower than i in the food chain. The stored energy changes imply that cropping for use in these manufactured goods is effected. If input p is used as an input for either more than one

species or more than one manufactured good, additional terms would be appended to (35).

There is a first order condition for each input used in each manufactured good and in each species. In total, there are $m P + n P + s$ first order conditions. The s is for the constraints in (27).

The raw inputs or resources are decision variables for the humans as they are allocated between manufacturing and the ecosystem. For the species, however, those resources are the parameters, since species have no control over them. Thus, as humans manipulate a resource to find its optimal use, comparative static changes are occurring in the ecosystem as it responds to the exogenous changes. The ecosystem seeks a new equilibrium which may not be what humans have in mind. An ecosystem externality, discussed below, is created.

At this juncture, a much simplified version of this model may be useful. Suppose there is a single raw input, one species, and one manufactured good. The raw input is divided between the manufactured good and the ecosystem so that

$$\bar{Y} = Y^Z + Y^h \quad (38)$$

The manufactured good is produced according to

$$Z = G(Y^Z, cA) \quad (39)$$

where cA is the cropped stored energy.

The stored energy of the species is

$$R^h = (1 - c)A(E, E^h, Y^h) \quad (40)$$

The human problem is to maximize $U(Z, R^h)$ subject to (38) - (40). If both Y^Z and Y^h are positive at the maximum, then first order conditions require

$$\frac{U_h}{U_z} = \left[\frac{\partial G}{\partial Y^Z} - c \frac{\partial G}{\partial cA} \frac{\partial A}{\partial Y^h} \right] / \left[(1 - c) \frac{\partial A}{\partial Y^h} \right] \quad (41)$$

This is a tangency condition between the human's marginal rate of substitution and the rate of product transformation between ecosystem amenities and the manufactured good. The numerator on the r.h.s. of (41) is the manufactured good's marginal product. It accounts for the fact that while manufactured output may tend to increase with increased raw input, this also means less raw input to the ecosystem and less ecosystem output into manufacturing which tends to decrease output. The denominator is the stored energy marginal output from changes in raw inputs.

Noninterior solutions are also possible and can be illustrated diagrammatically. Figures 7 and 8 show the production possibility frontiers in R^Z space (abc in Figure 7 and ab in Figure 8) and several possible

Figure 7

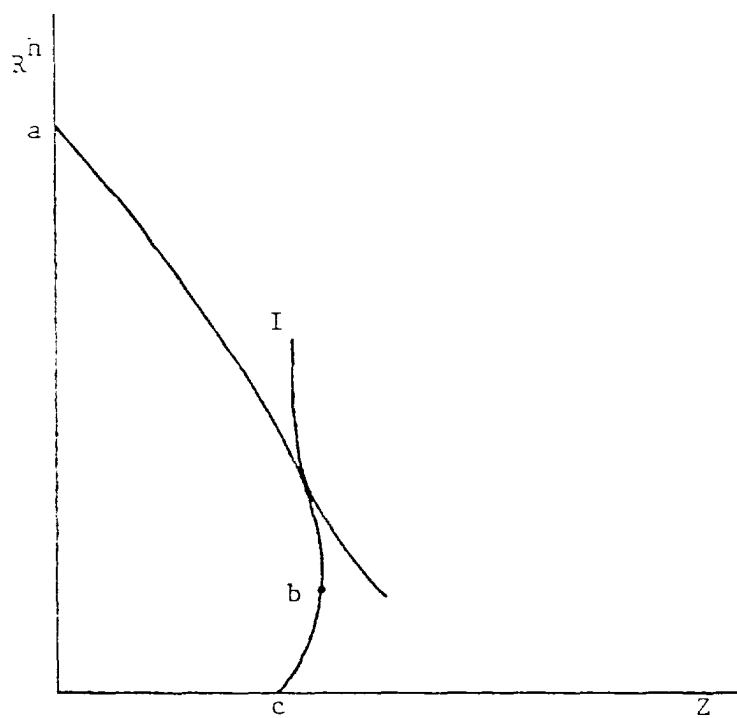
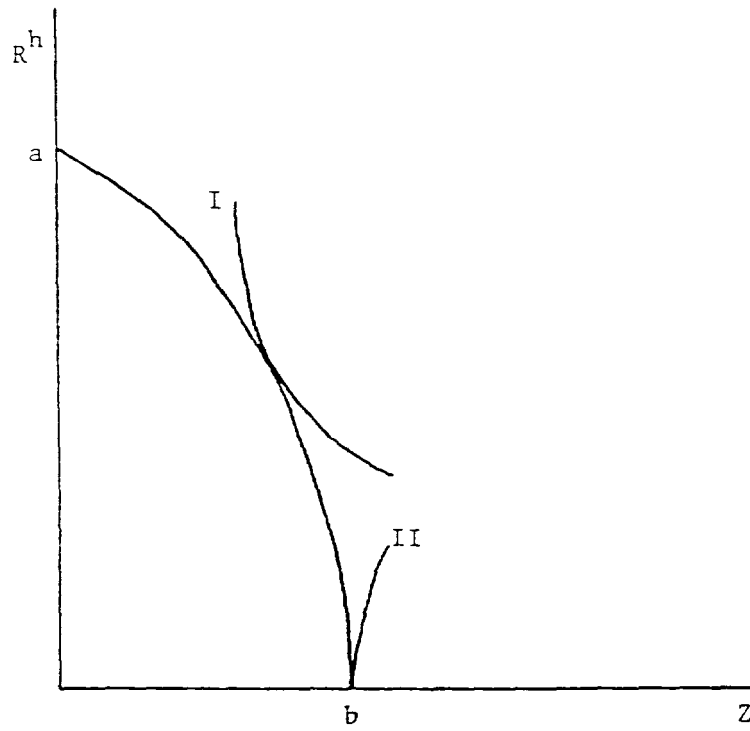


Figure 8



indifference curves. In Figure 7, the positively sloped portion, cb, indicates that raw input to the ecosystem creates higher stored energy in addition to more manufactured goods, since the stored energy can be cropped for inputs to the manufactured goods. Negatively sloped portions indicate a direct tradeoff between the use of raw inputs for manufacturing and ecosystems. Which shape obtains crucially depends on the term $\partial A / \partial Y^h$. The greater is this term then the more productive the ecosystem is in providing inputs to manufacturing from raw inputs. This then increases the possibility of a positive slope in the production possibility frontier, since the ecosystem can provide both inputs to manufacturing and to stored energy.

Indifference curve I in both Figures yield interior solutions. Indifference curve II in Figure 8 yields a solution where the ecosystem experiences no human intervention.

SECTION 7

ECOSYSTEM EXTERNALITIES

Above, the conditions which characterize an optimum distribution of resources among manufacturing and the ecosystem are presented. Resources are used as inputs for certain species, and these inputs can then enhance outputs from the species to humans. Inserting inputs to and cropping outputs from certain species will change stored energy levels and the availability of inputs and outputs to other species in the ecosystem. That is, $R_i^h \neq R_i$. Consequently, human intervention into any one species will have effects on many other species, as the intervention dictates a different ecosystem equilibrium. To the extent that stored energy levels differ in the new equilibrium in unexpected ways, an ecosystem externality is created. The stored energy levels may be expected to change, changed in unexpected ways, or certain species whose were not expected to change, did so.

The ecosystem externality can be contrasted to conventional externalities. An air polluting firm directly effects an argument in a consumer's utility function, that argument being clean air. The decrement in utility is clearly traceable to the externality source (although acid deposition may be an exception), but solutions to the problem are complicated because clean air is outside the market system. Human intervention into the ecosystem is an exogenous shock which causes that system to seek a new equilibrium. This gives rise to new stored energy levels, where these levels are arguments in a consumer's utility function. The intervention, which is tantamount to polluting in this example, must work its way through a complex general equilibrium system that is wholly external to the economic system. Thus, the effect on utility arguments are less direct for ecosystem externalities. And when links among species are unknown or poorly understood, the decrement (or increment) to utility due to an ecosystem externality may be untraceable to the original human intervention.

The following story provides a simple example of an ecosystem externality. Around the turn of the century, the citizens of Kern County, California, a rural area of farms and small towns, decided to do away with various predators that killed domestic animals and frightened children. Armed with shotguns, traps, and strychnine, they were very effective in decimating populations of skunks, foxes, badgers, weasels, snakes, owls, and hawks. In addition, they hired a team from the Department of Agriculture to exterminate all coyotes in the county. This was also successful. The myopic campaign took place over a period of two decades. Then, during a year when farmers were enjoying a bumper crop, hordes of mice appeared where they were not wanted. Their vast numbers, unchecked by

natural predators, were too much for the usual wild grains to feed; and the mice began to encroach on silos, barns, and homes. In places, the mice were ankle-deep, and people were killing them by the thousands. Distributing poisoned grain subdued the mice for a few months, but they eventually regrouped and descended on the villages. U.S. Highway 399 became so slippery from squashed mice that cars ran into ditches and "go slow" signs were erected. The affair was labelled by the U.S. Biological Survey as the greatest rodent infestation in U.S. history. One particular school had mice in every classroom, in all the waste paper baskets, and in some desks.

The infestation attracted owls, hawks, ravens, and vultures from other areas, but they were quickly done away with by the citizenry. The mice were continually in search of new food supplies, and, in 1926, occupied an area of 96 square miles. Finally, an expert from Washington in the U.S. Biological Survey, whose name was actually Piper, was given the exterminating duties. By counting burrows, he estimated his foe at 100 million strong. Using 40 tons of strategically situated strychnine alfalfa, he succeeded in his assignment. But not before Kern County lost over one million dollars in crops and property damage and spent \$5000 on poison.

The essence of this misadventure can be captured by the model herein. To the world of one raw input, one manufactured good, and one species, add two species. Species 1 can be a type of grain, species 2 mice, and species 3 a member of the owl family. The interaction among the species is a simple food chain with grain on the bottom and owls at the top. The societal utility function is

$$U(Z, R_1^h, R_2^h, R_3^h) \quad (42)$$

where grain is an intermediate good and not an argument. For the citizens of Kern County, it must have been the case that

$$U_{h2} < 0, \text{ and } U_{h3} < 0 \quad (43)$$

Of course, if a diverse citizenry is considered, and U^i is the utility function for the i th individual, $U_{h2}^i > 0$ and $U_{h3}^i > 0$ are reasonable possibilities, say for naturalists or birders. Nevertheless, (43) is assumed to hold for this example. Also, grain is assumed to provide no utility in and of itself, but is useful only in producing food or manufactured goods. Thus,

$$U_{hi} = 0 \quad (44)$$

Total raw inputs are accounted for by

$$\bar{Y} = Y^Z + Y_1^h + Y_2^h + Y_3^h \quad (45)$$

where Y_i^h is the input to the i th species, $i = 1, 2, 3$. Since there is only one raw input, double subscripting is unnecessary. The manufactured good is produced according to

$$Z = G(Y^Z, c_1 A_1) \quad (46)$$

where $c_1 A_1$ is grain output. For the mice, $y_2^h = 0$, at least until the time that strychnine is used. y_3^h is the input to the owls, but in this case where the input is destructive (poison, shotgun pellets) nothing is contributed to stored energy. Thus the associated energy price, $(E_3^h - E_3)$, is negative or $E_3^h < 0$. The stored energy functions from (32) are

$$R_1^h = (1 - c_1) A_1(E, E^h, X_{12}, Y_1^h) = (1 - c_1) \{E_{01} X_{01}(E, E^h, X_{12}(X_{23}(Y_3^h))), \quad (47)$$

$$R_2^h = (1 - c_2) A_2(E, E^h, X_{23}) = (1 - c_2) \{E_{12} X_{12}(E, E^h, X_{23}(Y_3^h)) - E_{23} X_{23}(Y_3^h)\} \quad (48)$$

$$R_3^h = (1 - c_3) A_3(E, E^h, Y_3^h) = (1 - c_3) \{E_{23} X_{23}(E, E^h, Y_3^h) - E_{34} X_{34} - E_3^h Y_3^h\} \quad (49)$$

interactions occurring external to the sphere of human influence and knowledge. While (48) is an ecosystem link between (47) and (49), that is, mice consume grain and are consumed by owls, it is not part of the human calculus. The energy prices, E , are unknown as well as how these prices adjust to exogenous shocks (human intervention) to the ecosystem; and the demand for grain by mice and the demand for mice by owls given by (31) in the general case are another unknown. Consequently, the feedback effects from the ecosystem seeking a new equilibrium will not be part of the human calculations.

Maximization yields the following condition:

$$U_z \frac{\partial G}{\partial Y^Z} = U_z \frac{\partial G}{\partial c_1 A_1} \frac{\partial A_1}{\partial Y_1^h} c_1 = U_z \frac{\partial G}{\partial c_1 A_1} \frac{\partial A_1}{\partial Y_3^h} c_1 + U_{h2} \frac{\partial R_2^h}{\partial Y_3^h} + U_{h3} \frac{\partial R_3^h}{\partial Y_3^h} \quad (50)$$

The first term is the manufactured good's marginal product weighted by the marginal utility for the good; the second term is the manufactured good's marginal product of ecosystem input (grain) weighted by the marginal

utility; and the third, fourth, and fifth terms are the marginal utility of the manufactured good's marginal product of grain input which is effected by the change in owls, the marginal utility of mice times the change in the stored energy of mice due to the change in owls, and the marginal utility of owls times the change in the Owls' stored energy due to their slaughter.

The values of Y^Z , Y_1^h , and Y_3^h that satisfy (50) provide the optimum solution for the citizenry of Kern County. The optimum is thwarted, however, because of a lack of information. The first two terms in (50) are accounted for by the citizens; that is, they are aware of how inputs of Y^Z and grain contribute to the production of manufactured good Z. Presumably, they also account for the last term, since they know that killing off owls will ostensibly improve their situation. Their knowledge ends here, however, and the County did not taken into account the effects represented by the third and fourth terms. These terms capture the ecosystem externality, as they form a wedge between marginal rates of substitution in consumption and the rates of product transformation. Examining these terms in more detail,

$$U_Z \frac{\partial G}{\partial c_1 A_1} \frac{\partial A_1}{\partial Y_3^h} c_1 = U_Z \frac{\partial G}{\partial c_1 A_1} c_1 [E_{01} \frac{\partial X_{02}}{\partial X_{12}} \frac{\partial X_{12}}{\partial X_{23}} \frac{\partial X_{23}}{\partial Y_3^h} - E_{12} \frac{\partial X_{12}}{\partial X_{23}} \frac{\partial X_{23}}{\partial Y_3^h}] \quad (51)$$

$$U_{h2} \frac{\partial R_2^h}{\partial Y_3^h} = U_{h2} (1 - c_2) [E_{12} \frac{\partial X_{12}}{\partial X_{23}} \frac{\partial X_{23}}{\partial Y_3^h} - E_{23} \frac{\partial X_{23}}{\partial Y_3^h}] \quad (52)$$

Expression (51) is the effect that killing owls has on the grain available for the manufactured good weighted by the marginal utility of Z. Inside the brackets are the chain of events in the ecosystem leading to less grain. More owls destroyed means less predation of mice and then more mice leads to less grain available. The first string of partials within the brackets accounts for grain's changed use of solar energy. Expression (52) is the effect that killing owls has on the mice and this is weighted by the marginal utility for mice.

All of the partials within the brackets in (51) and (52) were negative for Kern County. Moreover, $U_Z > 0$ and $U_{h2} < 0$ which means that both (51) and (52) are negative. Returning to (50), negative third and fourth terms, along with diminishing marginal utility and marginal product of Y^Z imply that too little of the raw input is being used directly in the product of the manufactured good, and too much is being used to destroy owls. This is reminiscent of the standard case of negative externalities. If production of a good produces negative externalities, the market will produce too much of this good from a welfare standpoint. In Kern County, there was too much production of a good (dead owls) that caused negative externalities in the

form of too many mice and too little grain.

Graphically, Figure 9 depicts the situation. In Z, R_3^h space, and for a given level of R_1^h , the perceived production possibility curve is Op . It is positively sloped, since more resources devoted directly to Z imply more Z and fewer resources for destroying owls, thus more owls. Curves I and II are community indifference curves with the direction of preference being north-west. The citizenry, using the perceived curve Op , kill off enough owls to attain R_3^{h*} which presumably leaves Z^* available and satisfies the usual tangency conditions. However, accounting for the negative externalities means that the true curve is Ot . Thus, when R_3^{h*} is attained, only Z^{**} is available: mice devour $Z^* - Z^{**}$. Utility is lower than expected, and a larger value for owl stored energy, or fewer resources devoted to killing owls, would be an improvement.

Figure 9

